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THE LIBERATION OF HEAT IN RESPIRATION

H. LUCILE MORIN

MORIN,H.

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Dr. G. J. Peirce.

THE LIBERATION OF HEAT IN RESPIRATION.

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A THESIS
SUBMITTED TO THE DEPARTMENT OF BOTANY AND THE COMMITTEE
ON GRADUATE STUDY OF THE LELAND STANFORD JUNIOR UNIVERSITY IN
PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF ARTS

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BY
H. LUCILE MORIN

MAY 1915

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Approved for the Department

Approved for the Committee on Graduate Study

Chairman

THE LIBERATION OF HEAT IN RESPIRATION

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1

Introduction

The oxidation of an organism --usually by the absorption of oxygen from without--which causes a chemical reaction in the organism, the final result of which is usually heat, carbondioxide and water is familiar to all of us under the term "respiration". It takes place at all times in all living cells and is so closely allied with vital activities that they are greatly injured when it is in any way impaired. The respiration is a constant process, it is more rapid at some times than at others. It can be noticed in resting seeds only by the most careful observation, but as soon as germination starts, respiration becomes more active, which activity results in a

greater liberation of the by-products. By measuring the final products one is able to determine how great the activity of respiration is under given conditions.

In a resting seed life is almost at a stand still. Growth has ceased for the time being, and there is no work to be accomplished by the embryo. If the temperature is very low and the seed very dry, even respiration has almost ceased. With an increase in temperature and moisture, however, respiration becomes more evident. This must of course be the case for the embryo plant even tho it is in a dormant state needs to be kept nourished. Great quantities of food material are stored either in the cotyledons or in the endosperm, largely in the form of starch.

Palladine* gives us the following equasion to express the reaction which takes place by the absorption of oxygen:

$$C_6 H_{10} O_5 + 6 O_2 = 6 C O_2 + 5 H_2 O.$$

This would make it seem that the action is a direct one, while in reality the carbon dioxide and water are the final results after a great many changes. He also tells us that under normal conditions the amount of oxygen absorbed is equal to the amount of carbon-dioxide liberated, but that external conditions such as heat, cold, wounding, light and dark are apt to change the amounts in relation to each other. These conditions, however, do not change the reactions which always have the same results. When

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*Palladine, V. Physiologie des Plantes, Paris, Masson et Cie, 1902. Chapt. Vll.

germination begins all of the energy which had been stored and inactive is set in motion. The embryo begins to grow and absorb food very rapidly and the respiration is likewise quickened. There is a continuous breaking down and rebuilding of the compounds in each cell. Chemical decompositions are the means by which the life processes are increased and germination is made possible.

Reynolds Green* tells us that the probable cause of events in respiration is that the oxygen in some way unites with the protoplasm rendering it unstable and initiating a series of decompositions which result in the successive formation of many bodies of less complex constitution, each

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*Green, Reynolds. Vegetable Physiology, London, J. and A. Churchill 1900, pages 127-128.

sucessive decomposition producing more simple ones until finally carbon dioxide and water are formed and liberated. The reconstruction of the protoplasm goes on at the same time, takes up the residue of the former structures and together with new food forms new protoplasm.

If the temperature is low, the breaking down proceeds but slowly, and the reconstruction is rapid, so that under these conditions the amount of oxygen absorbed is greater than the quantity of carbon-dioxide formed by its decomposition. Decomposition is carried on more easily at a higher temperature and its products are more numerous and simpler. It is possible that the protoplasm may combine loosely with the oxygen and transfer it to other substances present which are oxidized. In this way the protoplasm may act as an oxidizing agent without being

broken down itself. Carbon dioxide is thus the final term in a series of decompositions, of which the living substance is the seat and into which it may actually enter, the decompositions themselves being promoted by the access of oxygen. According to Palladine* the albuminoids are acted upon directly by the oxygen which the plant absorbs. The nitrogenous substances which result from the oxidisation of the albuminoids, combine with non-nitrogenous substances and form new albuminoids. Thus, because of the reserve material present which is free from nitrogen the quantity of albuminoids remains constant and the non-nitrogenous substances decrease gradually.

One of the proffs which he gives that the

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*Palladine, V. Physiologie des Plantes, Paris, Masson et *Cie*. 1902. Pages 160-166.

oxidation from respiration acts directly upon the albuminoids is that respiration is most active in the young and growing parts which are rich in protoplasm, hence in albuminoids and poor in all other organic substances. During the germination of seeds in the dark, the total quantity of albuminoids diminish as the yield of carbon dioxide increases slowly. The result of this is that plants which are poor in albuminoids respire more actively when at an advanced stage in growth than when younger. He has also found that during the period of mean germination when there is still a sufficient quantity of carbohydrates, the amount of carbon-dioxide freed increases in proportion to the quantity of indigestible albuminoids which are present.

During the germination of seeds in the dark a quantity of hydrogen is lost which unites

with the excess oxygen and is liberated in the form of water. Liaskovsky, who has worked on the question to some extent, has come to the following conclusions:

1- Very little water is formed during the part of germination of seeds.

2- The quantity of water which forms at low temperature is relatively greater than that which forms at higher.

3- There is not a definite relation between the hydrogen and carbon dioxide freed.

Thus the final results of the absorption of oxygen are accounted for and we see that a continual supply of energy is necessary for the

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*Palladine, V. Physiologie des Plantes, Paris, Masson et Cie. 1902 Page 160.

Liaskovsky, Germination des graines de Courge au point de vue chimique. Moscou, 1874, page 71.

maintainance of vital activities. Respiration increases the activities of the cell as it increases and as a result there are not only the chemical changes, but also a liberation of heat which appears to be the unavoidable accompaniment of the changes. Plants do not maintain a normal body temperature and for that reason any heat above the temperature of the surroundings is freed.

Only a very small portion of the energy liberated by respiration is converted into chemical or mechanical work. The food must be carried to different parts of the plants, the embryo must force itself out of the seed coat and usually into the ground, but aside from those two there is no work which a plant must do. Therefore all the excess energy is set free in the form of heat.

The amount of energy converted into work differs in different plants just as it does

in plants and animals. Animals must have energy for exercise, motion, circulation of the blood and so on to an innumerable list of activities, but even so there is still a great heat yield which is mere waste, as far as we can see at present.

The loss of heat by warm blooded animals is very great and is continuous as long as respiration takes place. The products of animal respiration vary with the food but the end products in both plants and animals are the same. The former are provided in all cases with means of discharging the excess heat. There are lungs, gills, radiation from the body, circulation of the blood and exhalation of the so called "breath."
Plants having no differentiated organs are able to lose heat only through radiation. As said above the liberation of the heat is not the same

at all times but differs with the activity of the protoplasm. In young plants and germinating seeds in which every cell reaches its greatest activity, in growth and food making, respiration is more active than in older parts where most of the cells are inactive and only a few of the new ones are carrying on the life processes.

11.

Apparatus and Methods.

The object of this piece of work was to construct a piece of apparatus which would be sufficiently sensitive to measure the heat yields of respiring organism and to take some measurements. Dewar* flasks have been used for about the past

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*Peirce, George J. A New Respiration Calorimeter. Botanical Gazette 46: 205-220, September 1908.

eight years and were successful for measuring the total heat yield and increase from day to day, but with them there was no way of getting at the liberation as it occurred. They made it possible to measure accumulated heat but could not measure the variations.

The calorimeter first consisted of a Dewar cylinder twelve inches in height and three and a half inches in diameter, a glass worm and a metal cup. The cylinder was made with a drain in the base into which the lower end of the glass worm fit. The worm was placed inside the cylinder and the metal cup inside the worm. A stream of water circulated through the worm which was in close contact with the cup on the inside and free on all others. The cylinder prevented absorption of any heat from without, so that any change in the temperature of the water could be traced directly to the cup. The object of

which the heat liberation was desired was placed in the cup as carefully as possible to prevent friction or undue warming by contact with the hands, the neck of the cylinder cotton plug and a stream run through the worm. Any heat liberated in the cup could be conducted only to the water in the coil of which the temperature was taken before and after circulation. The water was collected at the base of the coil by a dewar flask. Knowing the rate of flow and the change in the temperature of the water, it was very simple to calculate the amount of heat liberated. A tank above the apparatus in which the water was kept at room temperature and at a constant level furnished the supply and insured a uniform rate of flow.

The results from the use of this apparatus have been shown by Burnett Sanford, who was a stu-

dent in the department, to be about the same as the ones obtained in using the dewar flasks. The measurement was in both cases of accumulated heat. As shown by the corner there seemed to be an increasing amount until about the third day when the maximum was reached and from then on a decline.

The next step therefor was to have a constant stream by means of which one would be able to keep track of the change in temperature from minute to minute or from hour to hour as desired. The first constant stream was at the rate of two-hundred cubic centimeters of water per minute, but was found to be far too rapid. After several attempts it was regulated at 60 cc. per min. A dewar flask with a drain in the bottom was substituted for the closed one, a rubber tube with a pinch-cock was fastened to the drain and conducted the water to a near by sink. When the temperature was to be read,

the rubber was closed near the base of the flask by means of the pinch cock, a desired quantity of water collected and the temperature taken. With a constant stream, however, the heat was conducted away so rapidly that the results were not satisfactory. A four foot copper coil of [illegible] inch diameter was substituted for the glass worm and the results were better. It was hardly long enough to give the desired contact with the cup so a nine foot length of copper tubing was coiled and soldered into a cup a little larger than the first one which had been inside the glass worm. Thus both glass worm and metal cup were taken out. The inner surface of the new cup of coiled tubing was covered with nickle to prevent copper poisoning of the seeds put in to be tested. This was a great more efficient than any had been before because the seeds were in

direct contact with the coil. Heat was absorbed at once by the copper and taken up at once by the water in the coil.

At Mr. Burlingame's suggestion a coil of 1/8 inch tubing was made small enough to fit in a Dewar flask of about 500 c.c. capacity. It was very efficient for such a small quantity of seeds--as five [illegible]. This small coil can be set up and used just as the calorimeter now in use and the results are very satisfactory.

The variation in temperature was so little as indicated by a constant stream and use of thermometers that a thermal couple attached to a galvanometer was substituted for the therometers. The thermometers were graded to tenths of a degree centigrade and with care could be read to twentieths. The changes did not amount to as much as a twentieth of a degree at all times and consequently a great many fluctuations were entirely lost.

The readings as indicated by the galvanometer were made by the use of a scale placed in front of the minor which was diflected according to any change in current. The scale is ruled into twenty-five unit spaces each of which is again divided into ten. One half is marked in red figures, the other half in black, with the zero point in the center. One tenth of a calorie of heat diflects the minor six tenths of a unit space. A tenth of a unit space which is one of the smallest markings on the scale, therefore, indicates a change in temperature of one sixtieth of a degree centigrade. It can be read to just half of that which is one, one-hundred and twentieth of a degree centigrade. Thus it is now possible with the thermal couple to record very minute changes and with the constant stream to see them recorded as they happen. The heat is conducted

away as liberated so any change in temperature is due to a reaction which has taken place just prior to the diflection of the mirror.

Thus with one small change after another, the calorimeter has evolved into the apparatus as it is now set up and shown in the accompanying diagram.

The thermal cylinder is the same one that was used in the original apparatus with the drain closed and the water made to flow out through the top. By the entrance of the water at the bottom of the coil first, the coil will be kept full at all times. A second much smaller coil is placed in the cup made by the first so that the reeds surround the inner and are surrounded by the outer and all are in contact with one or the other. A continuous stream of water from a tank above in which the water is kept at a constant level is circulated

through each coil at the rate of fifteen cubic centimeters a minute, making in all thirty cubic centimeters pass around the seeds once a minute. After the water has passed through the coils it is conducted to a smaller thermal cylinder of about seventy-five cubic centimeters capacity. In it the water level is kept constant by means of a hydrostatic pump. The water being let in at the bottom and taken out at the top assures a change from minute to minute, the arm of the thermal couple which is attached to the galvanometer is in this cup just below the bottom of the pump. Another similar cylinder of the same size, and supplied with the same kind of pump, is so placed that the water which flows into it passes thence through the coil. The other arm of the thermal couple is placed in

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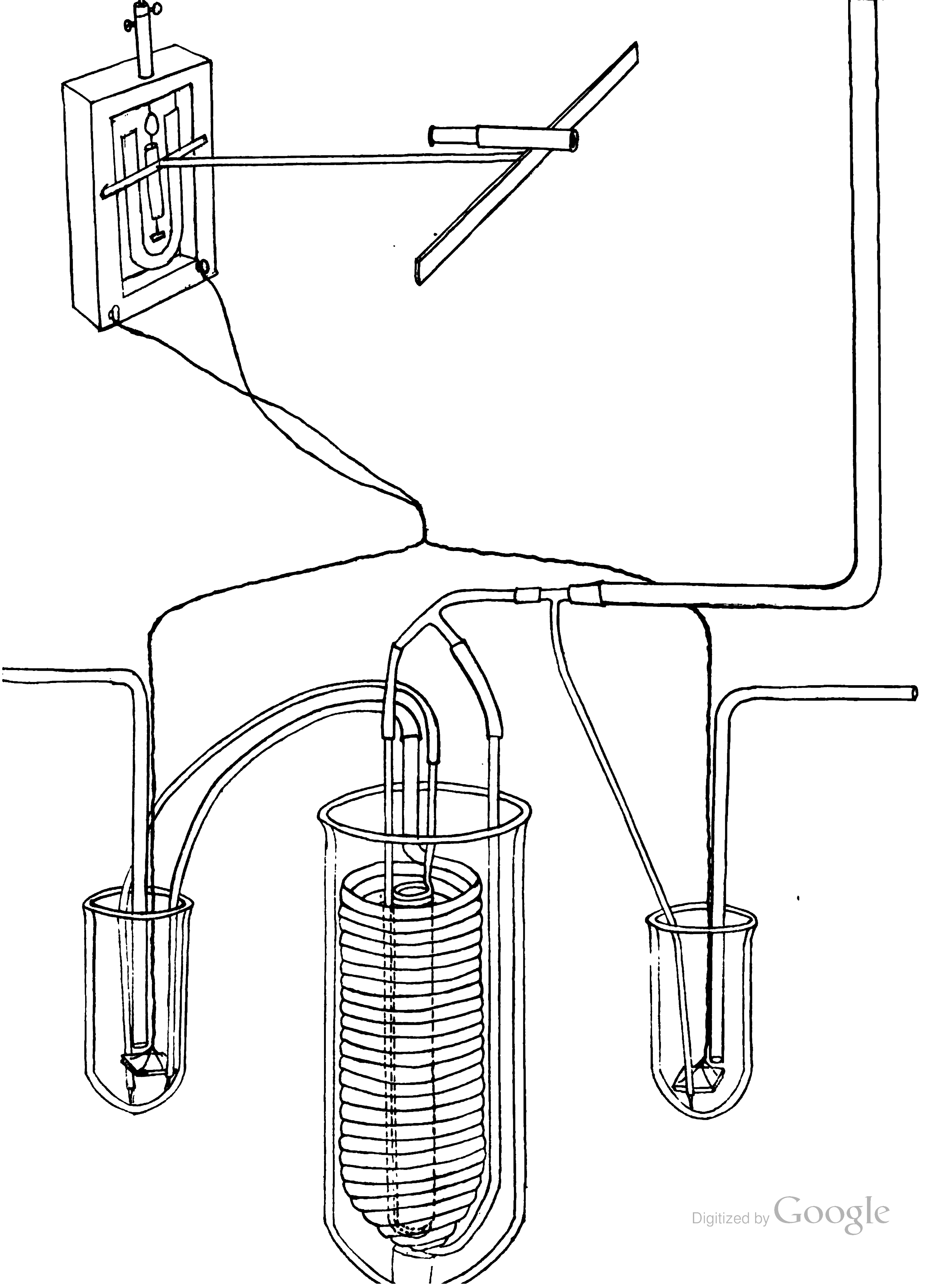


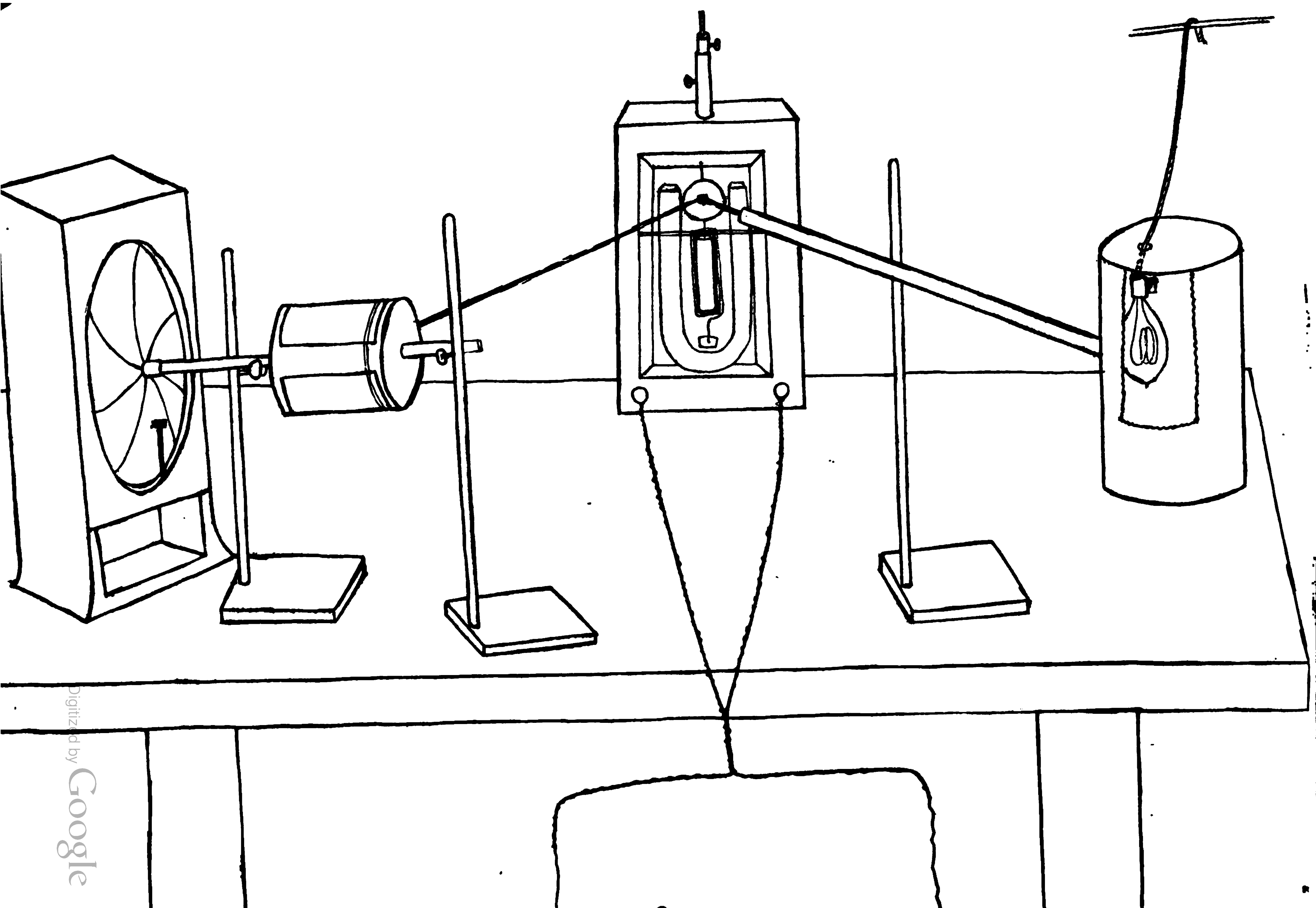
this cup. Thus the water bathing one arm of the thermal couple passes through the coils and is collected in the other small cylinder where the difference in temperature if any, will affect the other arm of the thermal couple and consequently diflect the mirror of the galvenometer.

With this apparatus we have has some results which are rather surprising when compared with the first ones. A great deal of assistance in its construction given by Mr. Scott and Mr. Brown, students in the department. To them also is given the credit of constructing a self-recording apparatus which is also shown in an accompaning diagram. An electric light in a tin can throws a beam of light, in which the rays are made nearly parallel by a series of diaphragms in a tube, so that it strikes the center of the mirror in the galvanometer. The beam is reflected upon bromide paper covering a revolving drum

at the opposite side. The light makes a line on the paper when it is developed and any diflection of the mirror causes a curve in the line. The drum revolves on an axis which is attached to the center of the dial of a self-recording thermometer. The axis is supported by a set of wheels on each end of the wheels on each end of the drum and the drum makes one revolution a week. The change in temperature, as indicated by the line shows the changes from day to day but the turning is so slow that the hourly records hide each other. It will be a great improvement to have a drum which revolves once a day and on which the records can be written from hour to hour and compared with the readings taken from the scale. The paper on the drum can be marked by spotting the place where the beam falls with a small minor and marking an ink spot.

This self recording apparatus must be set up in a dark room to protect the bromide paper. A small room has been built of lumber frame work covered with black tar paper and is very successful in keeping the light out. Whenever light is necessary a red globe is used.

With this calorimeter one of the first results to be noticed was that the heat liberated did not increase steadily up to a certain point and then decline, but that there were constant fluctuations the highest one being reached between the second and fourth hours after germination has started. The liberation was uniform rather than increasing. The second and third days were more nearly constant than the first, the third day showed decrease and the fourth day some variations, resting at zero at some times and liberating heat at others. At times the seeds seem to absorb heat from the water. This, however, I believe was due to the



Selfrecording Galvanometer.

cooling of the room quickly at night and the water slowly. Toward morning the water would also have cooled and the room would have warmed up again. Thus there was not a balance of these temperatures except during the day. The ideal condition for this apparatus as for all others, would be a constant temperature room in which the water temperature would also remain uninfluenced by weather conditions or by steam heat turned on in a laboratory during the day.

These experiments at first seemed to show that heat was absorbed by the seeds before germination actually started. This point was watched very closely and appeared in nearly every case. The drop lasted from one-half to one hour at the end of which time the heat was liberated up to a maximum point which comes, as mentioned above, about four hours after germination has started. Precautions have been taken to [illegible] the seeds,

waste and calorimeter all of the same temperature before starting any experiment. It was of some interest to note that seeds could not be evolved entirely by placing them in the calorimeter and running the water around them. This was tried on several occasions but there was nearly always a small liberation of heat. The mirror would not come to rest at exactly the zero point. Another method has therefore been used. The can of seeds --air and water tight-- was placed so that it would be in a constant changing flow of water. After it had been there several days the seeds were weighed out in fifteen gram lots, care being taken not to handle them, were done up in separate packages and placed in a desiccator over glacial phosphoric acid which absorbed the excess moisture. The desiccator was placed in an oven kept cool by a constant flow of water through the jacket. The calorimeter itself

was cotton plugged and run until everything was equal in temperature and it read exactly zero. Into the cup made by the coil sixty cubic centimeters of water were run from the supply. Care has been taken at all times not to touch any part of the apparatus after the seeds were put in, so that any changes in temperature could be traced only to the germination of the seeds.

III.

Data of Experiments.

The tables below show some typical readings with the apparatus set up as described. They indicate the changes in the amounts of heat liberated. The average amount of heat liberated by fifteen grams of peas is 7 calories per minute for the first twelve hours. The second day the rate is about 2 calories per minute and the third day about 1. The liberation has always

been less at night, presumably because the water and apparatus became cooler. The average for three days, however, supposing the rate to be uniform and the amount evenly distributed is [illegible] calorie per minute. This gives the result of 214.84 calories of heat liberated by one organ during a period of three days. The heat liberated by combustion of the same amount would be about 744.75 calories.

A comparison of this result with that obtained by Bonnier* in 1892 is rather interesting. He found that a kilogram of seeds liberated 53 calories of heat per minute during germination. That gives us .053 cal. per gram min., 3.54

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*Bonnier, G. Recherches sur la chaleur vegetale An. Sci. Nat. Bot. VII 18: 1[illegible], 1893.

calories per gram hour and 256.38 calories per gram in three days. This makes my figures a little lower than his. On Tuesday March 23, 1915, the apparatus was started and allowed to run over night in order to equalize all temperatures. The can was filled with sixty cubic centimeters of water from the supply. Fifteen grams of air-dry peas were placed in the cooling oven. Wednesday at 9:00 A.M. the calormiter stood at zero. Room temperature 1[illegible]° C. water and feed temperature 17.0° C. The peas were put into the coil at 9:[illegible] A.M. with the following result:

Time	Scale	Room Temp.	Water Temp.
9:05 A.M.	.2	19°C.	18°C.
9:08	.3		17.9°C.
9:11	.4		
9:14	.45		
9:17	.5	19°C.	17.9°C.
9:20	.4		
9:25	.5		
9:30	.5		
9:35	.4		
9:40	.6	19°C.	17.9°C.
9:50	.8		
10:00	.6		
10:10	.8		
10:20	.9		
10:40	.7		
11:00	.9	19°C.	18.1°C.
12:15	1.05		
1:15 P.M.	.9	20°C.	18.4°C.
2:40	.6	20°C.	18.7°C.

The following table is one which shows the change during several days. It was started at 10:15 A.M. on Tuesday, April 23, 1915 and run until the following Saturday:

Time	Scale	Calories	Time	Scale	Calories
Tuesday			Thursday		
10:25A.M.	.1black	½	9:45 A.M.	0	0
10:27" "	.5 "	2½	10:45	.3black	1½
10:35" "	.1 "	½	11.15	.3 "	1½
10:50" "	.05"	¼	1:30 P.M.	.4 "	2
10:55" "	.0 "	0	4:10	.25 "	1¼
11:00" "	.2 "	1	4:30	.6 "	3
11:03" "	.1 "	½	Friday		
11:05" "	.3 "	1½	8:55 A.M.	.8 red	4
11:10" "	.4 "	2	9:55	.3 "	1½
11:30" "	.6 "	3	10:40	.1 "	½
12:00 M.	.5 "	2½	11.15	.1black	½
12:30 "	.7 "	3½	2:00 P.M.	0	0
1:00 P.M.	.4 "	2	3:30 P.M.	.1black	½
1:30 " "	.1 "	½	4:30 P.M.	0	0
2:10 " "	.2 "	1	Saturday		
3:00 P.M.	.5 "	2½	9:00 A.M.	.3 red	1½
3:15 " "	.5 "	2½	11:00A.M.	0	0
4:15 " "	.8 "	4	12:00A.M.	.1 lb.	½
4:34 " "	.4 "	2	3:00 P.M.	0	0
Wednesday					
8:50 A.M.	.3 red	1½			
9:20 " "	0	0			
10:15" "	6 black	3			
11:15" "	.5 "	2½			
11:45" "	.5 "	2½			
12:05 M.	.4 "	2			
1:30 P.M.	.4 "	2			
2:55 " "	.5 "	2½			
3:40 " "	.5 "	2½			
4:30 " "	.5 "	2½			
5:30 " "	.3 "	1½			

The heat yield of five grams of tad-poles was found to be just about as much in one hour as that of fifteen grams of peas during the fourth and fifth hours after germination has started. That is about one-hundred and thirty calories. The experiment was again set up just exactly the same using five grams of peas in 120 c.c. of water rather than the tad-poles. The heat liberated the first day, however, was not of sufficient quantity to change the mass of water covering the seeds so no change in temperature was indicated. Upon drawing off the water the morning of the second day there was a marked rise in temperature and for the following two days there was a uniform liberation of about a calorie per minute. The two charts below show the changes due to five grams of tadpoles and fifteen grams of beans. The heat yield of beans is almost identical to that of peas. Tad-

poles at room temperature, apparatus at zero. Tad-poles put into coil by means of a spoon and kept active by stirring gently twice during the time with a thermometer placed in the inner coil.

Time	Scale	Calories	Time	Scale	Calories
10:A.M.	0	0	10:20	.4 bl.	2
10:03	.1 bl.	½	10:25	.2	1
10:04	.4	2	10:30	.6	3
10:05	.5	2½	10:45	.6	3
10:08	.4	2	10:47	.4	2
10:10	.2	1	10:50	.3	1½
10:12	.1	½	11:00	.4	2
10:15	.2	1	12:00	.2	1
10:17	.4	2	1:30	.5	2½

Fifteen grams of small red beans give the following table:

Time	Scale	Calories	Time	Scale	Calories
10:30	0	0	10:53	.5	2½
10:34	.3	1½	10:56	.8	4
10:35	1.5	7½	11:00	.7	3½
10:37	.5	2½	12:00	.6	3
10:38	.2	1	1:15	.5	2½
10:40	.3	1½	2:30	1.1	5½
10:42	.8	4	3:45	.2	1
10:47	.7	3½	3:50	1.8	9
10:50	.4	2	5:15	1.2	6

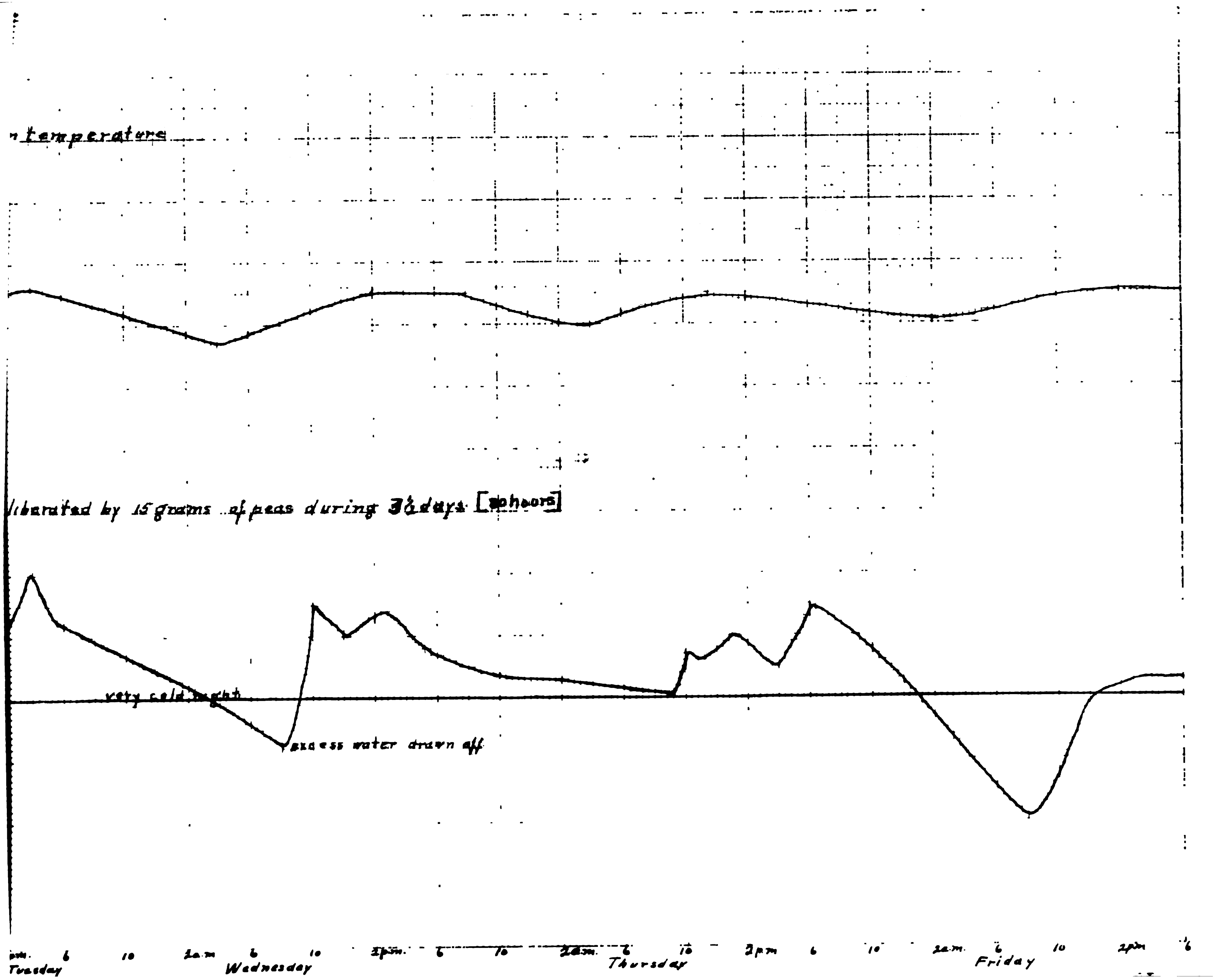
A mouse weighing ten grams was used to test the heat liberation of warm blooded animals. It had been in captivity for twenty-four hours, with plenty to eat, before it was forced into the coil with some difficulty. When once in, the opening of the cylinder was closed with a wire screen and the apparatus cotton plugged as usual. The temperature of the water rose immediately and settled back to a rather uniform rate of liberation as shown by the chart below. The average heat liberation per minute was 8 2/3 calories; the total for the hour 520 calories.

Time	Scale	Calories	Time	Scale	Calories
10:05A.M.	2bl.	10	11:36	1.8bl.	9
11:08	2.2	11	11:39	1.6	8
11:10	1.8	9	11:42	1.7	8½
11:12	1.7	8½	11:45	1.6	8
11:15	1.4	7	11:48	1.5	7½
11:18	1.4	7	11:51	1.8	9
11:21	1.3	6¼	11:54	1.6	8
11:24	1.5	7½	11:57	1.6	8
11:27	1.4	7	12:00	1.7	8½
11:30	1.5	7½	12:03	1.6	8
11:33	1.6	8	12:05	1.7	8½

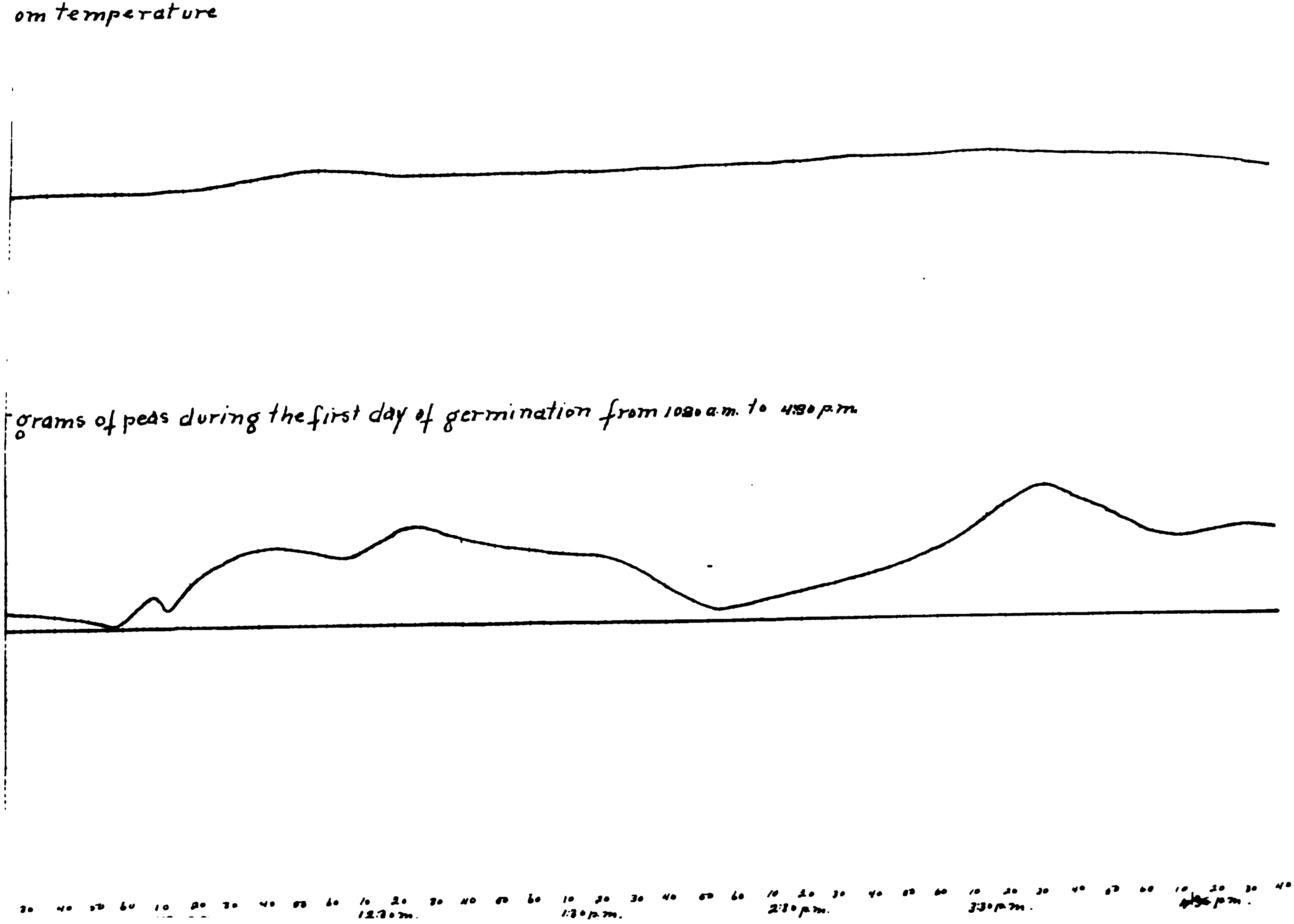
1V.

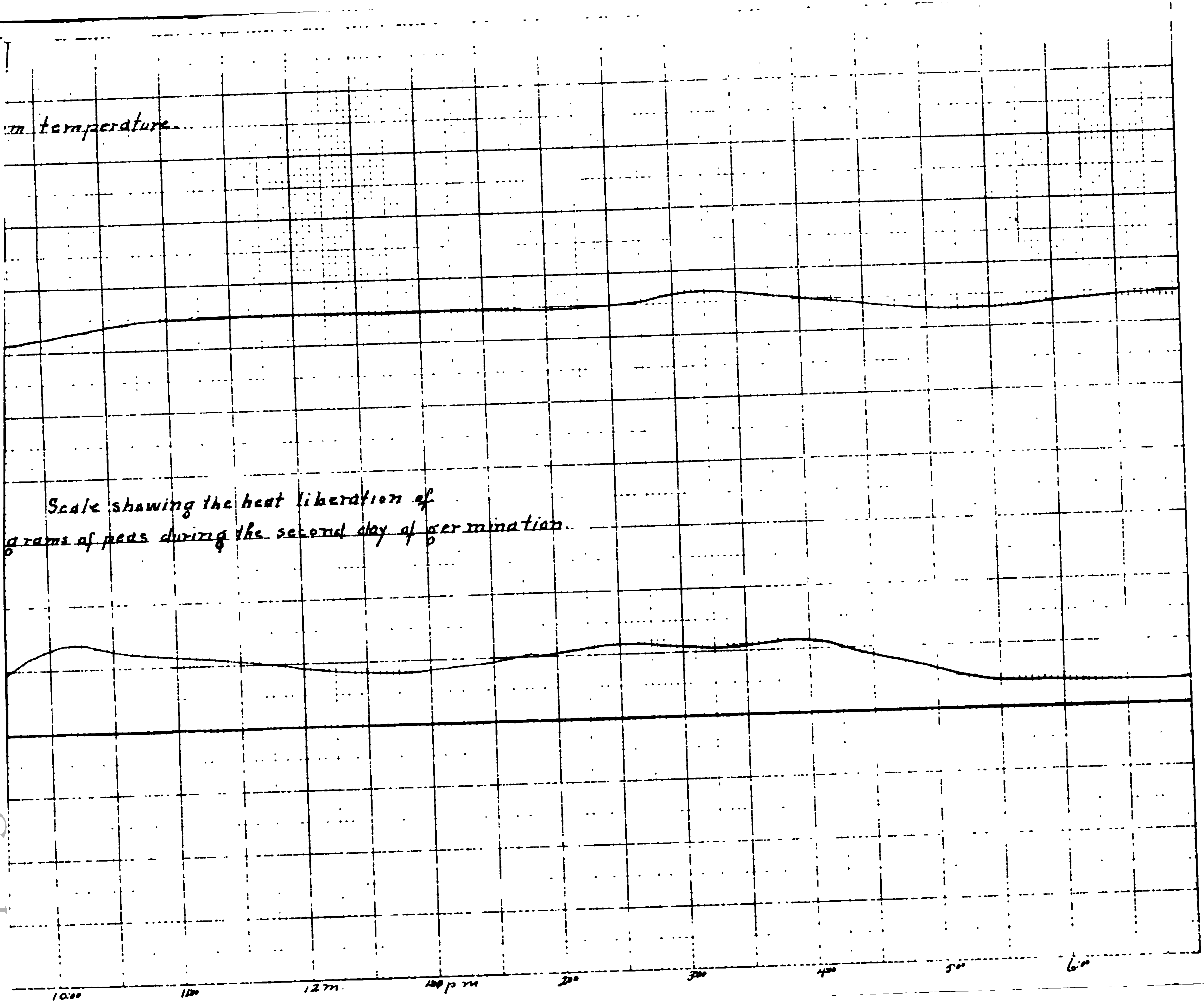
Conclusion.

These experiments show again that the release of energy in the form of heat is much greater than the organism can possibly use. The energy of an organism varies with the food, covering, exercise, activity and other functions. The heat is a waste product just as the carbon dioxide and water are waste products of the chemical reactions. It is necessary for the well being of every plant or animal to have some means to rid itself of these by products which would be very harmful if allowed to collect. In some organisms the heat maintains a normal body temperature while in others this is not necessary, but an excess above this normal or even the surrounding temperatures in the lower organisms must be gotten rid of. It would cause fever and a consequent weakening if not



n temperature
liberated by 15 grams of peas during 3½ days [[illegible]hours]
very cold night
excess water drawn off
pm. 6 10 2a.m 6 10 2pm. 6 10 2a.m. 6 10 2pm 6 10 2a.m. 6 10 2pm 6
Tuesday
Wednesday
Thursday
Friday

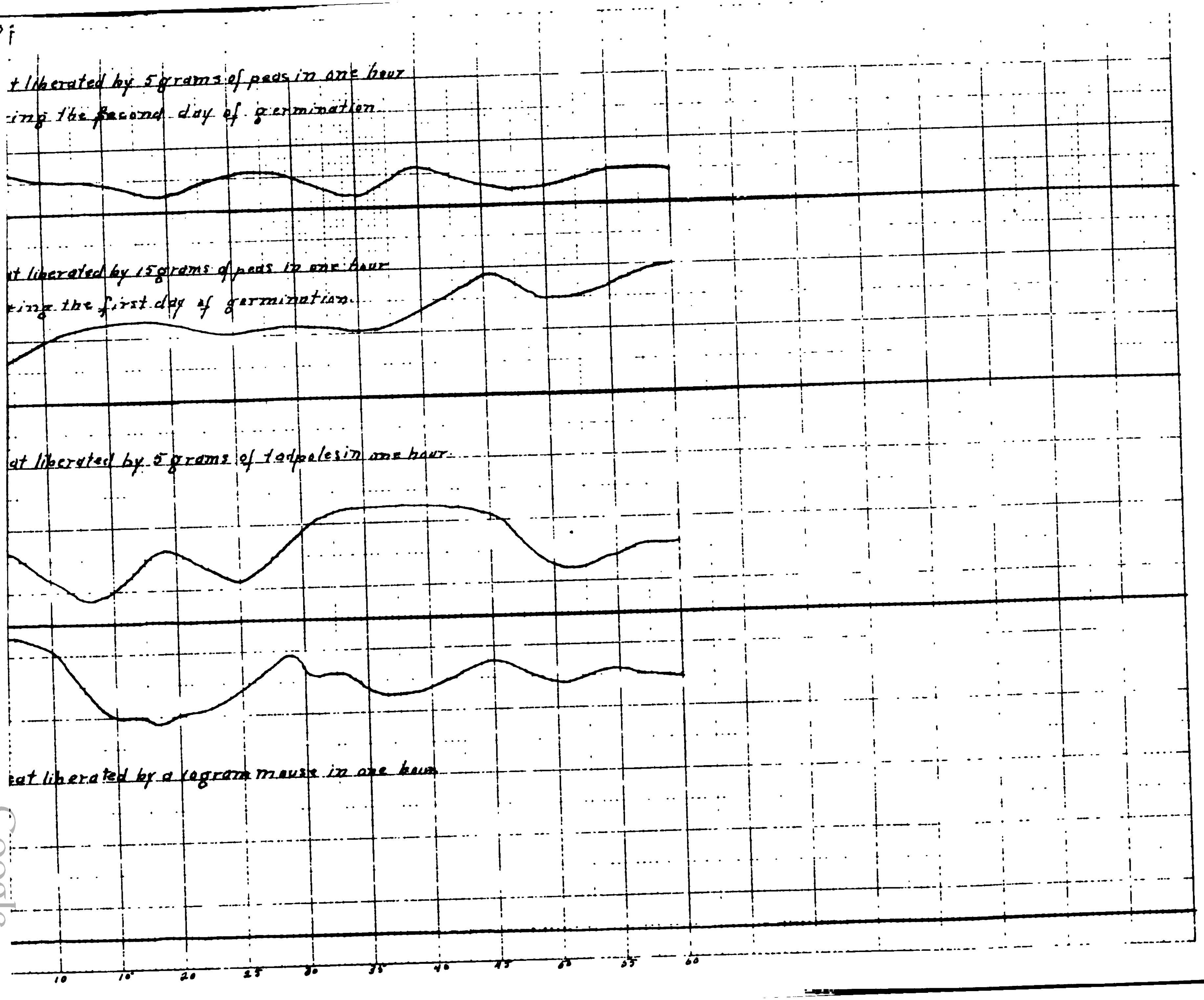

om temperature
grams of peas during the first day of germination from 10:30 a.m. to 4:30 p.m.
0
30 40 50 60 10 20 30 40 50 60 10 20 30 40 50 60 10 20 30 40 50 60 10 20 30 40 50 60 10 20 30 40 50 60 10 20 30 40
12:30 p.m.
1:30 p.m.
2:30 p.m.
3:30 p.m.
4:30 p.m.



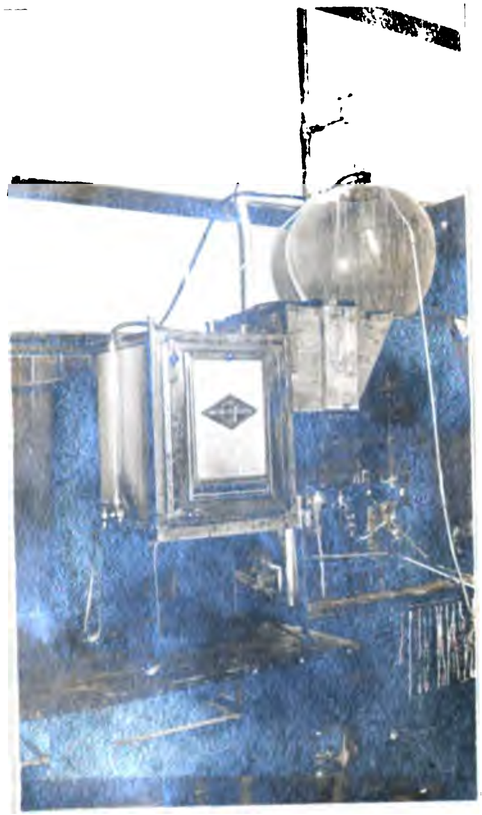
m temperature.

Scale showing the heat liberation of
grams of peas during the second day of germination.

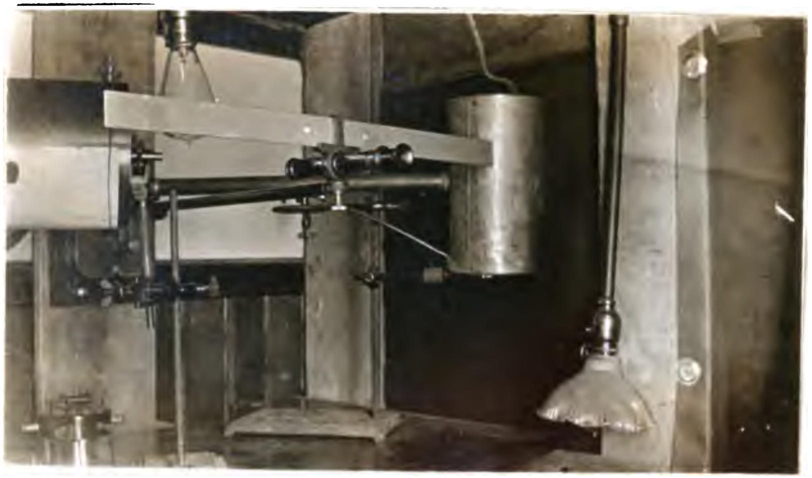
Fig. I


t liberated by 5 grams of peas in one hour
ing the second day of germination
t liberated by 15 grams of peas in one hour
ing the first day of germination
at liberated by 5 grams of tadpoles in one hour
eat liberated by a 10 gram mouse in one hour
10
15
20
25
30
35
40
45
50
55
60

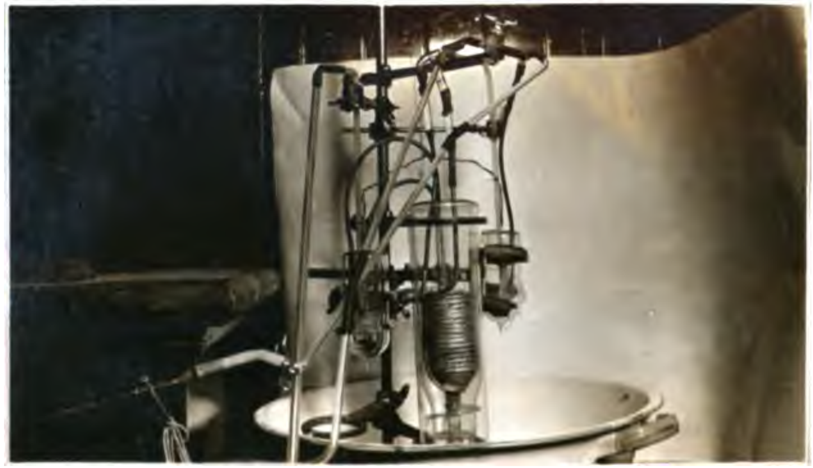
be expected to extend and clarify this subject, and it would appear that the apparatus thus described, and which has been developed as narrated above, puts us in possession of the means of attacking the problem of heat liberation and heat removal in a quantitative manner.



Cooling oven, pumps and water supply for calorimeter.



Self recording galvanometer.



Calorimeter.

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